The Feeding Habits and Ecology of *Dentalium entale stimpsoni* Henderson[1]

(Mollusca : Scaphopoda)

BY

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(7 Text figures)

INTRODUCTION

For more than a century it has been known that scaphopods are carnivores, feeding primarily on Foraminifera and, occasionally, on bivalve spat (Clark, 1849). The capture of prey has been credited to the captacula (Clark, *op. cit.*; Morton, 1959; Dinamani, 1963; Gainey, 1972). The purposes of this study are to determine if the scaphopod *Dentalium entale stimpsoni* is a selective feeder, and the effect of predation on its food source. Relationships between *D. e. stimpsoni*, the prey, and the environment are presented.

Dentalium entale stimpsoni Henderson, 1920, ranges from Nova Scotia to North Carolina at depths of 15 to 2295 m (La Rocque, 1953) and is considered a subspecies of *D. entalis* Linnaeus, 1758, found in Europe (Henderson, 1920).

MATERIAL and METHODS

Since distribution of *Dentalium entale stimpsoni* is patchy, and population densities are low, a two-step sampling procedure was necessary. A ponar grab (WILDCO; Saginaw, Michigan; 1/20 m^2) was used for sampling the benthos and sediments associated with *D. e. stimpsoni*, and a triangular dredge (GM Co., New York, N. Y.; 38 × 38 × 61 cm) was used to collect specimens of *D. e. stimpsoni* along the line of the ponar grab sites.

Three grabs (designated X.1, X.2, X.3) were taken in a line about 70 m apart at the stations described below. The top screen of the grab was hinged, and could be lifted for sampling undisturbed surface sediments. Immediately upon grab retrieval (to minimize error), the temperature of the surface sediment was taken from the upper 2 cm of sediment (which *D. e. stimpsoni* inhabits). Samples of the Foraminifera and the surface sediment were also taken from the upper 2 cm of sediment. The remainder of the grab material was retained for identification of the macrobenthos.

Stations 1, 2, and 3 are shown in Figure 1. During this study, a total of 4 samples were taken at these stations. Sample 1 (12 July 1971) was taken at the inner Johns Bay station and sample 2 (13 October 1971) at the outer Johns Bay station. Both samples 3 (13 September 1972) and 4 (22 November 1972) were taken at the Damariscove Island station, which has been divided into 3 areas (Figure 2): the upper slope (3-U), the middle slope (3-M), and the lower slope (3-L).

In addition to the ponar grabs taken at station 3-M in samples 3 and 4, other ponar grabs were taken at that station on various dates. All grabs taken there (a total of 30) were used to estimate the population density of *Dentalium entale stimpsoni*.

In samples 1, 2, and 3 the previously described two-step sampling procedure was followed, and all sampling was done where *Dentalium entale stimpsoni* was present. In sample 4, however, one ponar grab was taken in each slope area of the Damariscove Island station, rather than all 3 grabs in the middle slope area. Grabs 4.1 (upper slope), 4.2 (middle slope), and 4.3 (lower slope) were taken for comparison of environmental factors and faunas. No dredging was done in sample 4.

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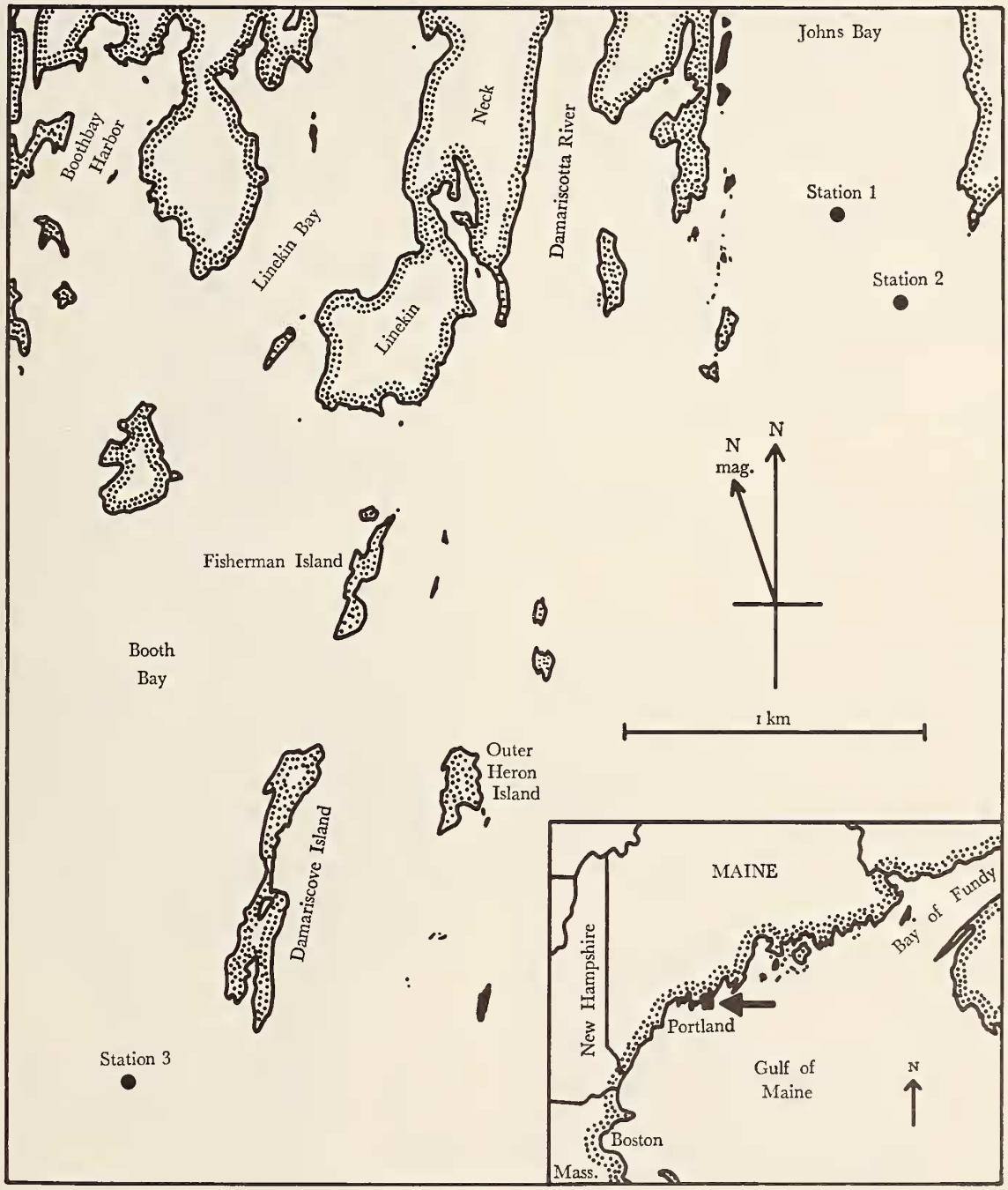
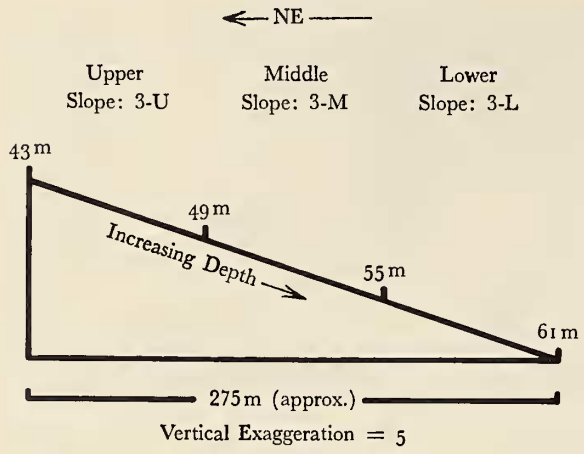


Figure 1

Chart of the Boothbay Region, including Stations 1, 2, and 3



Sampling Areas of Station 3 (off Damariscove Island)

Figure 2

Station 3 Sampling Areas

Foraminifera and other potential food organisms in the sediment were sampled with a modified 5 cc syringe. With the end of the syringe cut off, a core 2 cm deep with a volume of 1.8 cc could be obtained. In samples 1 and 2 the material was preserved in 70% isopropyl alcohol, washed on a sieve (nylon mesh) with 73 μm openings and dried. A dissecting microscope aided in the identification of the organisms. In samples 3 and 4, formalin (5%, neutralized with baking soda) was used as a preservative, and rose bengal stain was added to facilitate the separation of living and dead Foraminifera (rose bengal will stain any protein in the test, but not the test itself). Samples were later washed on a sieve (nylon mesh) with 73 μm openings and placed in a Petri dish for wet sorting and identification.

Sediment grain size analysis followed the modified AS TM Standard D 422-63 method for hydrometer and sieve (Anonymous, 1963). Organic content was estimated by determining the loss of weight upon ignition of samples for 4 hours at 440° C. The samples were weighed before and immediately thereafter.

Identifications of Foraminifera were based on the work of Loeblich & Tappan (1964) and on foraminiferal papers for the fauna of the Gulf of Maine and adjacent waters (Parker, 1952; Vilks, 1969; Sen Gupta, 1971).

Macrobenthic organisms were retained on a sieve (stainless steel with 1 mm openings), preserved in 10% neutralized formalin, and stained with rose bengal. Species diversity indices of the macrobenthos and the Foraminifera were calculated from equations 1 and 8 given by Pielou (1966) for type A collections (in which all organisms can be sorted and counted).

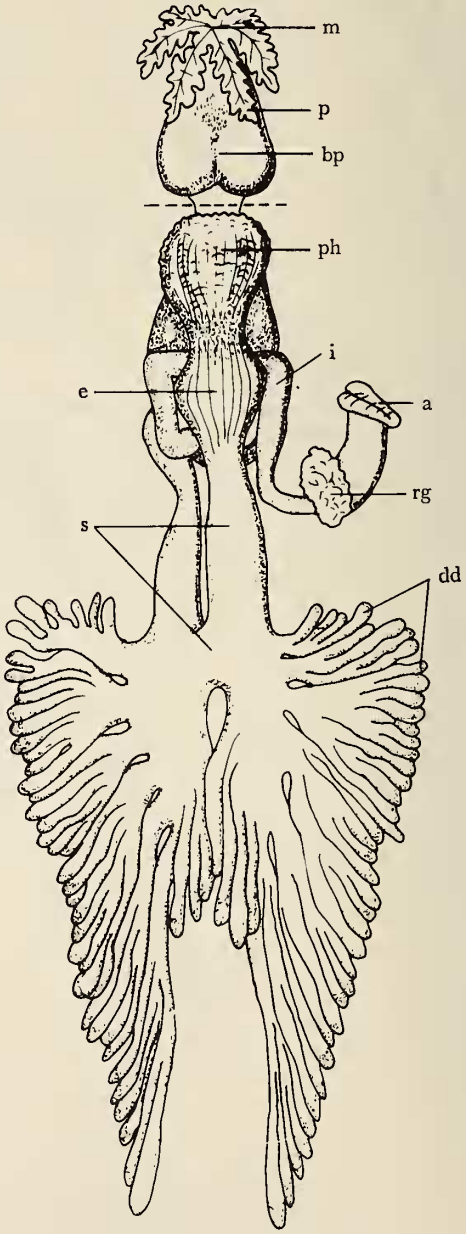


Figure 3

Digestive System of *Dentalium*

a – anus bp – buccal pouch dd – digestive diverticula
e – esophagus i – intestine m – mouth p – palps
ph – pharynx rg – rectal gland s – stomach
(after Lacaze-Duthiers, 1856: plt. 8, fig. 1)

The diversity per individual (H) is defined by Pielou (1966: 131) as "the degree of uncertainty attached to the specific identity of any randomly selected individual." If the distribution of the organisms among the species in a collection is nearly uniform, then the degree of uncertainty associated with any individual is near its maximum. But if the distribution of organisms among the species is very uneven, the degree of uncertainty is very small. Furthermore, when the number of organisms remains unchanged, the degree of uncertainty increases or decreases with respective increases and decreases in the number of species. The relative diversity (J) is a measure of the "evenness with which the individuals are divided among the species in any collection" (Pielou, *op. cit.*: 141) and is calculated by dividing the diversity per individual by the maximum possible diversity.

Specimens of *Dentalium entale stimpsoni* collected for analysis of their gut contents were immediately placed in 10% neutralized formalin. In the laboratory, food organisms were removed from the gut by dissection. The digestive system is diagrammed in Figure 3. Food ingested by the palps and mouth is held in the buccal pouch until it passes through a constriction into the pharynx. A radula, located in the pharynx, efficiently grinds the food organisms into small pieces before they are passed into the esophagus and stomach. Consequently, gut contents are identifiable in the buccal pouch, prior to entering the pharynx. Therefore, in searching for ingested organisms, the contents of excised buccal pouches were carefully examined (the dotted line in Figure 3 indicates where the buccal pouch was dissected from the remainder of the digestive system). In samples 1 and 2, gut contents were dried on filter paper for sorting and identification. In sample 3, they were placed in 5% neutralized formalin and stained with rose bengal. After staining, the buccal pouch contents were sorted and identified while immersed in water.

RESULTS

Environment: At the Damariscove Island station, the temperature of the surface sediment was 7° C on 31 July 1972; 8° C on 22 November 1972; and 2° C on 26 February 1973; suggesting a yearly temperature range of less than 10° C.

Grain size distributions of the sediments at stations 1, 2, and 3 are shown in Figures 4, 5, and 6, respectively, following the method outlined by Shepard (1954). Mud is defined as the fraction smaller than 63 μm (silt and clay). The sediments at the Johns Bay stations (1, 2) were sand, while those at the middle slope area of the Damariscove Island station (grabs 3.1, 3.2, 3.3, 4.2) were predominantly sand. Grab 3.2 has a lower ratio of sand to mud, having been taken at the deeper end of station 3-M. The upper slope area (grab 4.1) was predominantly gravel, while the lower slope area (grab 4.3) was mud (clayey silt). A sediment gradient is present at station 3, changing from gravel to sand to mud with increasing depth. *Dentalium entale stimpsoni* was found only in sandy sediments.

Table 1 summarizes the other environmental factors at stations 1, 2, and 3. Organic content of the sediment was approximately the same at stations 1, 2, 3-U and 3-M (1.2 to 2.1%). Only at station 3-L (the lower slope area of the Damariscove Island station) did the percentage of organic matter increase substantially to 5.5%.

Table 1

Environmental factors at Stations 1, 2, and 3
H – diversity per individual; J – relative species diversity

Environmental factor	Stations				
	1	2	3-U	3-M	3-L
% Organic matter in sediment	1.4	1.2	2.1	1.6	5.5
Associated macrobenthos:					
Organisms/m²	—	4 047	580	5 760	7 200
H	—	0.70	0.93	0.77	0.43
J	—	0.53	0.96	0.51	0.32
Foraminiferal fauna:					
Organisms/cc	—	—	129	100	60
H	—	—	1.11	1.03	0.48
J	—	—	0.64	0.84	0.61

The macrobenthos associated with *Dentalium entale stimpsoni* at the outer Johns Bay station (2) and the Damariscove Island station (3) was quantitatively analyzed, and the data are also given in Table 1. The number of organisms/m² was calculated from ponar grab data, and it increases with increasing depth at the Damariscove Island station. Faunal density at station 2 compares favorably with that of the middle slope of the Damariscove Island station (3-M). The diversity per individual (H) decreased with increasing depth at station 3, while the diversity per individual of the macrobenthos at station 2 approximated that at station 3-M. The relative diversity followed a similar pattern.

In summary, there was a progressive increase of faunal density and decrease of faunal diversity of the macrobenthos at the Damariscove Island station with increasing

Table 2

Macrobenthos identified from Stations 2, 3 - U, 3 - M, and 3 - L

	Stations			
Mollusca	*2*	*3-U*	*3-M*	*3-L*
GASTROPODA				
Lora scalaris (Möller, 1842)	x		x	
Retusa obtusa (Montagu, 1808)			x	
BIVALVIA				
Arctica islandica (L., 1858)			x	
Astarte subequilatera Sowerby, 1854	x	x	x	
Astarte undata Gould, 1841	x		x	
Cerastoderma pinnulatum (Conrad, 1831)	x	x	x	
Crenella decussata (Montagu, 1808)	x		x	
Hiatella sp.		x	x	
Mya arenaria L., 1758	x			
Nucula delphinodonta Mighels, 1842	x		x	x
Nucula proxima (Say, 1822)	x		x	x
Nucula tenuis Montagu, 1808			x	
Nuculana pernula (Müller, 1779)			x	
Periploma papyratium (Say, 1822)		x	x	x
Tellina agilis Stimpson, 1858			x	
Thyasira gouldi (Philippi, 1845)			x	
Venericardia borealis (Conrad, 1831)	x			
Yoldia myalis (Couthouy, 1838)			x	
Sipunculida				
Golfingia minuta (Keferstein, 1862)	x			
Phascolion strombi (Montagu, 1804)			x	
Annelida				
POLYCHAETA				
Aglaophamus sp.	x			
Aglaophamus circinata (Verrill, 1874)	x			
Ammotrypane aulogaster Rathke, 1843			x	
Ancistrosyllis groenlandica McIntosh, 1879				x
Anobothrus gracilis (Malmgren, 1866)	x	x	x	x
Aricidea quadrilobata Webster and Benedict, 1887			x	
Brania clavata (Claparède, 1863)	x			
Caulleriella sp.	x			
Cirratulus cirratus (Müller, 1776)		x	x	x
Clymenella zonalis (Verrill, 1874)	x		x	x
Cossura sp.			x	
cf. *Diplocirrus hirsutus* (Hansen, 1879)			x	
Dysponetus pygmaeus Levinsen, 1879		x		
Euphrosine armadillo Sars, 1851	x			
Exogone verugera (Claparède, 1868)	x			
Gattyana cirrosa (Pallas, 1766)	x			
Goniada maculata Oersted, 1843	x		x	x
Glycera capitata Oersted, 1843	x		x	
Harmothoe extenuata (Grube, 1840)		x		
Harmothoe imbricata (L., 1767)	x	x		
Heteromastus filiformis (Claparède, 1864)				x
Laonice cirrata (Sars, 1851)			x	
Lumbrineris fragilis (Müller, 1776)		x	x	x
Lumbrineris tenuis (Verrill, 1873)	x			
Melinna elisabethae McIntosh, 1922	x	x	x	
Myriochele heeri Malmgren, 1867	x		x	x
Nephtys ciliata (Müller, 1776)			x	
Nephtys incisa Malmgren, 1865	x		x	x
Nereis sp.	x			

Table 2 [continued]

	Stations			
	2	*3-U*	*3-M*	*3-L*
Nereis grayi Pettibone, 1956			x	
Ninoe nigripes Verrill, 1873			x	x
Owenia fusiformis Delle Chiaje, 1841			x	x
Paraonis gracilis (Tauber, 1879)			x	
Pholoe minuta (Fabricius, 1780)	x		x	
Polycirrus sp.			x	
Polydora socialis (Schmarda, 1861)	x		x	
Polyphysia crassa (Oersted, 1843)		x		
Phyllodoce mucosa Oersted, 1843	x		x	
Potamilla reniformis (Müller, 1771)	x			
Rhodine sp.			x	x
Rhodine loveni Malmgren, 1866			x	x
Sabellides sp.	x	x		
Scalibregma inflatum Rathke, 1843	x		x	
Scolelepis squamata (Müller, 1806)		x		x
Scoloplos acutus (Verrill, 1873)			x	x
Spio filicornis (Müller, 1776)	x			
Sternaspis sp.			x	x
Terebellides stroemi Sars, 1835			x	
Trichobranchus gracilis Malmgren, 1866			x	
Arthropoda				
PYCNOGONIDA				
Nymphon sp.		x		
CRUSTACEA				
MALACOSTRACA				
Mysidacea				
Erythrops erythropthalma (Göes, 1863)	x			
Cumacea				
Diastylis sculpta Sars, 1871	x			
Diastylis quadrispinosa Sars, 1871	x		x	
Eudorella hispida Sars, 1871			x	
Eudorella truncatula (Bate, 1856)	x			
Pseudocuma longicorne (Bate, 1858)			x	
Isopoda				
Cyathura polita (Stimpson, 1855)			x	
Edotea triloba (Say, 1818)	x			
Amphipoda				
Aeginina longicornis (Kröyer, 1842)	x			
Ampelisca spp.	x	x	x	
Byblis sp.			x	x
Corophium sp.	x			
Ericthonius rubricornis (Stimpson, 1853)	x	x		
Leptocheirus pinguis (Stimpson, 1853)	x			
Melita sp.				x
Monoculodes sp.			x	
Paradulchia typica Boeck, 1870			x	
Unciola irrorata Say, 1818	x	x	x	
Echinodermata				
OPHIUROIDEA				
Amphipholis squamata (Delle Chiaje, 1828)		x	x	
Chordata				
ASCIDIACEA				
Bostrichobranchus pilularis (Verrill, 1871)	x			

depth, which suggests a more stable community at the upper slope area, and a less stable community at the lower slope area. *Dentalium entale stimpsoni* was found only in the area of moderate faunal density and diversity.

A species list of macrobenthos and their occurrence at stations 2 and 3 is found in Table 2. Organisms which could not be identified to genus (due to damage, etc.) were omitted from the table, but their respective taxonomic units were included in species diversity calculations.

The density and diversity of the live foraminiferal fauna at the Damariscove Island station (3) are summarized in Table 1. In contrast to the inverse relationship demonstrated by the macrobenthos, the Foraminifera showed a direct relationship between the faunal density, which decreased from 129 organisms/cc to 60 organisms/cc, and the diversity per individual, which also decreased. Numerous factors could have been responsible for the unexpected decrease in faunal density.

The fauna changed radically from the upper slope area to the lower slope area (Table 3). The upper slope fauna consisted chiefly of calcareous Foraminifera, which were absent in the lower slope area. Conversely, the scant occurrence of agglutinated Foraminifera in the upper slope area contrasted with their abundance in the lower slope.

Table 3

Abundant species of live foraminifera in the upper (3-U), middle (3-M), and lower (3-L) slope areas of station 3, expressed as percentages

Species	Stations 3-U	3-M	3-L
Calcareous foraminifera:			
Elphidium spp.	25	12	0
Islandiella islandica (Nørvang)	24	8	0
Cibicides lobatulus (Walker and Jacob)	13	9	0
Bucella frigida (Cushman)	6	4	0
Globobulimina auriculata (Bailey)	1	8	0
Agglutinated foraminifera:			
Reophax atlantica (Cushman)	9	21	19
Urnulina sp.	8	9	57
Eggerella advena (Cushman)	4	5	2
Trochammina spp.	0	3	17
Miscellaneous	10	21	5

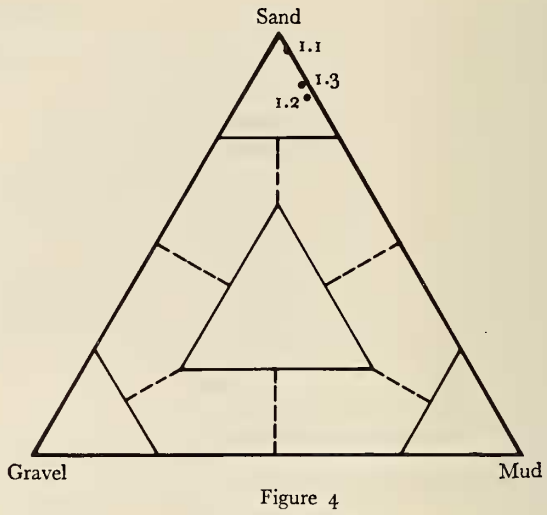


Figure 4

Station 1 Sediments

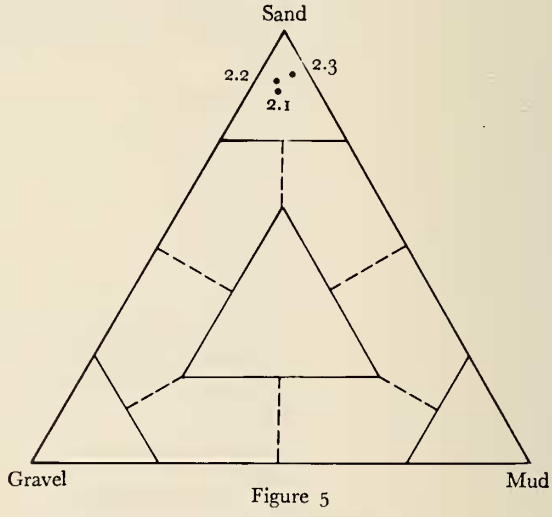


Figure 5

Station 2 Sediments

The calcareous and agglutinated faunas were also found consistently off Portsmouth, New Hampshire by Phleger (1952), who divided them into the sand facies (found in sandy and gravelly sediments), and the mud facies. Different community structures of the 2 faunas could explain the progressively decreasing population density. The change from gravel to sand to mud implies a change from a high current energy environment to a low current energy environment. Decreasing current energy with increasing depth, and changes in other related environmental factors, such as depth, temperature, salinity, the quantity

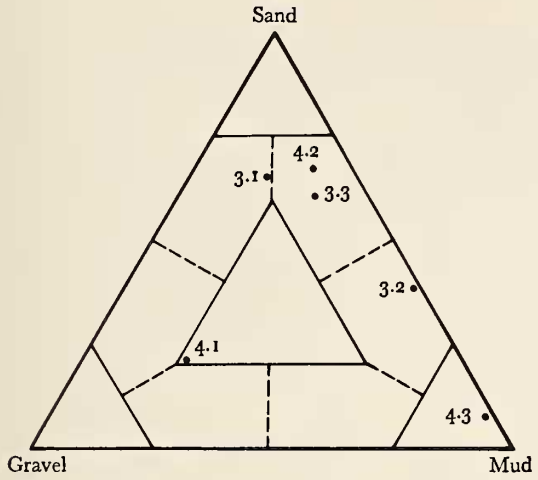
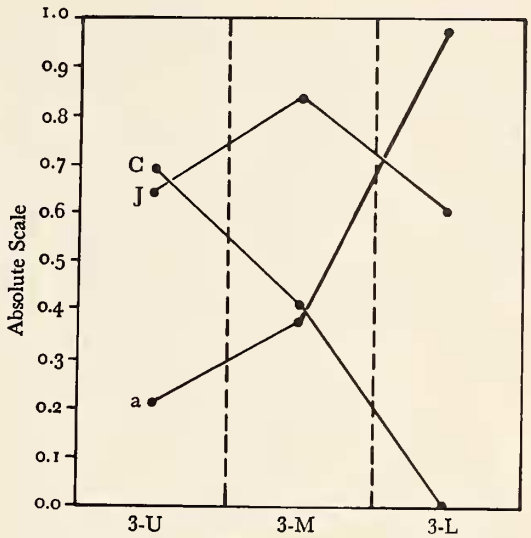


Figure 6

Station 3 Sediments



Sampling Areas of Station 3
(off Damariscove Island)

Figure 7

Abundance of Calcareous (c) and Agglutinated (a) Foraminifera as a function of their occurrence in the slope areas of Station 3, plotted on an absolute scale. J is the relative species diversity of the total foraminiferal populations

and depth of oxygen penetration into the sediment, and sediment grain size could also affect population density.

The abundances of the important calcareous and agglutinated Foraminifera in the 3 slope areas are plotted on an absolute scale in Figure 7. Relative species diversity indices are also plotted. Although the diversity per individual of the foraminiferal population decreased with increasing depth, the relative diversity did not; it is approximately the same in the upper slope areas, and higher in the middle slope area. The relative diversity indices in the upper and lower slope areas are approximately equal because each area contains a fauna which is adapted to that area's environment. The middle slope area, however, is an ecotone, and contains numbers of both faunal assemblages. The high relative diversity index of that area reflects the presence of species from both faunas.

Food and Feeding Habits: *Dentalium entale stimpsoni* is a carnivore, ingesting organisms and rejecting inorganic materials from the sediment. In sample 3 the food organisms (all types) in the buccal pouches averaged 31 per individual, while sand grains not incorporated into foraminiferal tests averaged 3 per individual. Fine sediment particles and detritus were never found in the buccal pouches. Selectivity is probably expedited by the presence of sensory cells in the terminal bulbs of each captaculum (Morton, 1959).

No evidence was found to indicate that either mucus from the captacula (Gainey, 1972) or buccal pouch secretions was causing artificially high counts of stained Foraminifera in the gut. Had secretions been able to enter the foraminiferal tests, they most likely would have entered through the aperture, the largest opening in the test. Entry into the aperture would have caused consistent staining in the terminal chamber of each of the ingested foraminiferal tests, a phenomenon which was not observed. A large percentage of the foraminiferal tests was stained in one or more adjacent chambers, but not necessarily in their terminal chambers.

Table 4 summarizes data collected in samples 1 and 2, in which living and dead Foraminifera were not distinguished. The average percentage of each important organism found in the buccal pouches of *Dentalium entale stimpsoni* and the sediment are given. Eleven *D. e. stimpsoni* were examined and found to contain 231 food organisms in sample 1, while 6 *D. e. stimpsoni* were found to contain 80 food organisms in sample 2.

In sample 1 the percentages of food organisms found in the sediment were determined by examination of 8 foraminiferal cores from 3 ponar grabs. Comparison of the cores demonstrated that one from each grab was sufficient to obtain accurate and reproducible results; thus,

Table 4

Percentages of food organisms in the buccal pouches (b. p.) and sediment in Samples 1 and 2

Species	*Sample 1*		*Sample 2*	
	% b.p.	*% sed.*	*% b.p.*	*% sed.*
Calcareous foraminifera:				
Islandiella islandica (Nørvang)	18	9	27	18
Elphidium spp.	28	10	17	15
Cibicides lobatulus (Walker and Jacob)	3	4	6	48
Quinqueloculina spp.	6	<1	16	<1
Bucella frigida (Cushman)	4	4	5	1
Agglutinated foraminifera:				
Eggerella advena (Cushman)	15	12	5	4
Reophax atlantica (Cushman)	1	51	1	7
Other food organisms:				
Eggs	13	1	12	1
Ostracods	<1	<1	1	1
Bivalve spat	<1	<1	2	<1
Marine mites	1	<1	0	0
Miscellaneous	9	5	8	3

in samples 2, 3, and 4, one core per grab was examined.

As shown in Table 4, eggs, ostracods, and marine mites were prey of *Dentalium entale stimpsoni,* in addition to the Foraminifera and bivalve spat previously reported (Clark, 1849; Morton, 1959). Exact identification of the eggs commonly found in the gut was not possible, but they are belived to be those of an invertebrate, possibly a turbellarian.

Data in Table 4 indicate that there was selection of food by *Dentalium entale stimpsoni* at both stations; *D. e. stimpsoni* selected *Quinqueloculina* spp. and eggs, but avoided *Reophax atlantica.* Each of the other food organisms was eaten in approximately the same proportion in which it was found in the sediment, with the exception of *Cibicides lobatulus,* which was eaten in the same proportion in sample 1, but not in sample 2. The apparent change of feeding habits in relation to *C. lobatulus,* the consistent selection of *Quinqueloculina* spp. and eggs, and the consistent rejection of *R. atlantica* indicated that *D. e. stimpsoni* is a selective feeder. The sampling procedure in samples 3 and 4 was changed to attempt to determine the factors responsible for selective feeding.

Staining with rose bengal aided the separation of live and dead organisms in both the sediment samples and the buccal pouch contents of *Dentalium entale stimpsoni* in sample 3. Vertical distribution of living Foraminifera and other food organisms in the sediment at station 3-M was examined by dividing a foraminiferal sample horizontally into four $\frac{1}{2}$ cm sections. All live organisms, including eggs, were equally distributed in the 4 sections, eliminating the possibility that unequal vertical distributions were responsible for the feeding patterns of *D. e. stimpsoni.*

Table 5

Sample 3. Percentages of live food organisms in the buccal pouches (b. p.) and sediment (sed.)

Species	b.p.	sed.
Calcareous foraminifera:		
Islandiella islandica (Nørvang)	94	41
Elphidium spp.	82	27
Cibicides lobatulus (Walker and Jacob)	93	27
Globobulimina auriculata (Bailey)	92	55
Quinqueloculina spp.	97	55
Bucella frigida (Cushman)	83	28
Virgulina spp.	82	23
Agglutinated foraminifera:		
Cribrostomoides spp.	100	26
Eggerella advena (Cushman)	100	54
Reophax atlantica (Cushman)	100	45
Other food organisms:		
Ostracods	90	8
Bivalve spat	92	28

Percentages of live food organisms in the sediment and the buccal pouches of *Dentalium entale stimpsoni* in sample 3 are given in Table 5; *D. e. stimpsoni* (98 specimens containing 3 070 food organisms) consistently selected living organisms.

Table 6 summarizes the percentages and characteristics of the food organisms found in the sediment and the buccal pouches of *Dentalium entale stimpsoni* in sample 3. The composition and texture of the exterior of each organism are listed. Texture, ranging from smooth to rough, is characterized as smooth, moderately smooth, average, moderately rough, and rough. The 3rd column gives the percentage of each food organism in the buccal pouches, while the 4th column gives the percentages of each species of food organisms alive in the sediment, based on the total number of food organisms alive in the sediment. The percentage of each species alive in the sediment is given because it is from the live population that *D. e. stimpsoni* selects its food (Table 5). The selective index (S. I.) is the ratio of the percentage of the organism in the buccal pouches to the percentage of that organism alive in the sediment (% b. p./%sed.). Indices greater than 1.0 indicate positive selection, while indices smaller than 1.0 indicate negative selection.

As in samples 1 and 2 (Table 4), *Dentalium entale stimpsoni* actively selected *Quinqueloculina* spp. and eggs as food, but rejected *Reophax atlantica. Cibicides lobatulus* in the buccal pouches occurred in about the same ratio as the *C. lobatulus* in the sediment in sample 3, suggesting that sample 1 data may be more indicative of the feeding habits of *D. e. stimpsoni* than sample 2 data. Minimal ingestion of *C. lobatulus* in sample 2 might have been due either to a high ratio of empty tests washed into the environment, or to the fact that *C. lobatulus* is an epizoite, frequently found on algae or the surface of the sediment. Only in the latter case would it occasionally be in the feeding zone of *D. e. stimpsoni.* However, since live and dead Foraminifera were not distinguished in samples 1 and 2, the cause could not be definitely determined.

Since *Dentalium entale stimpsoni* can detect live Foraminifera and separate them from empty tests, it follows that the captacula detect the extended cytoplasm of the Foraminifera. The presence of cytoplasm which extends outside the test is the only difference between a living and

Table 6

Sample 3. Food organisms, their important characteristics, and their percentages of occurrence in the buccal pouches of *Dentalium entale stimpsoni* and the sediment.

org., organic; mod. sm., moderately smooth; ave., average texture; mod. rh., moderately rough; S.I., selective index.

Species	*Composition*	*Texture*	*% b.p.*	*% sed.*	*S.I.*
Calcareous foraminifera:					
Islandiella islandica (Nørvang, 1945)	$CaCO_3$	mod. sm.	32.3	4.9	6.6
Elphidium spp.	$CaCO_3$	ave.	15.4	6.9	2.2
Cibicides lobatulus (Walker and Jacob, 1798)	$CaCO_3$	ave.	14.0	5.7	2.4
Globobulimina auriculata (Bailey, 1851)	$CaCO_3$	mod. sm.	5.9	4.1	1.4
Quinqueloculina spp.	$CaCO_3$	smooth	5.1	0.7	7.3
Bucella frigida (Cushman, 1922)	$CaCO_3$	ave.	2.1	2.3	0.9
Virgulina spp.	$CaCO_3$	ave.	0.6	1.7	0.3
Agglutinated foraminifera:					
Cribrostomoides spp.	sand-org.	rough	3.0	0.8	3.7
Eggerella advena (Cushman, 1922)	sand-org.	mod. rh.	1.6	2.3	0.7
Reophax atlantica (Cushman, 1944)	sand-org.	rough	0.8	10.2	<0.1
Trochammina spp.	sand-org.	mod. rh.	<0.1	1.5	<0.1
Urnulina sp.	inorganics	mod. rh.	0.0	4.6	0.0
Other food organisms:					
Eggs	org.	mod. sm.	8.1	1.3	6.2
Ostracods	$CaCO_3$-org.	rough	2.6	0.4	6.5
Bivalve spat	$CaCO_3$-org.	ave.	1.7	0.2	8.5
Marine mites	org.	mod. rh.	0.5	0.0	—
Copepod eggs	org.	mod. sm.	0.3	19.1	<0.1
Nematodes	org.	smooth	<0.1	16.8	<0.1
Small worms	org.	ave.	<0.1	4.4	<0.1

a recently dead foraminifer. Sensory cells in the terminal bulbs of the captacula are probably responsible for detection of the cytoplasm.

Calcareous Foraminifera comprised most of the food of *Dentalium entale stimpsoni* in samples 1, 2, and 3: their abundance in the gut was far greater than that of the agglutinated Foraminifera or other organisms. In sample 3, only 1 of the calcareous genera had a selective index much lower than 1.0, while 4 of the remaining 6 genera has selective indices greater than 2.0. Test microstructure and the amount of cytoplasm present outside the test are probably responsible for the abundance of calcareous Foraminifera in the gut.

The calcareous genera (except *Quinqueloculina*) are of the suborder Rotaliina and have perforate tests, while the agglutinated Foraminifera are of the suborder Textulariina, most of which have imperforate tests. The presence of perforations allows cytoplasm to flow out of the test at many locations, and more completely envelop it. Cytoplasmic envelopment of the test by imperforate Foraminifera is not possible, however, since the cytoplasm can only stream from the aperture. Therefore, the amount of cytoplasm around the outside of the test is greater in the perforate Foraminifera, and there is a greater chance of detection by the captacula.

Although *Quinqueloculina* spp. has a very high selective index (7.3), it is an imperforate foraminifer of the suborder Miliolina and has a very smooth, porcelaneous test. Since the cytoplasm can exude only from the aperture, the high selective index might be due to large amounts of cytoplasm outside the test, or to the very smooth test surface.

The feeding habits of *Dentalium entale stimpsoni* upon agglutinated Foraminifera further demonstrate the detection of organic matter by the captacula. *Reophax atlantica* has a test of coarse sand with little organic matter, and was eaten only occasionally. Yet *Cribrostomoides* spp., with a test of coarse sand and much organic matter, and *Eggerella advena*, with a test of fine sand and much organic matter, were often ingested. If the captacula were able to distinguish organic materials, then *Cribrostomoides* spp. and *E. advena* would have been more easily detected, due to the high percentage of organic matter in their tests, while *R. atlantica* would have been infrequently detected, for lack of much organic matter. This pattern was present in sample 3 data. When *R. atlantica* was ingested, it was probably due to the detection of the pseudopods rather than detection of the test. It was noted that all agglutinated Foraminifera ingested by *D. e. stimpsoni* in sample 3 were alive (Table 5).

Bivalve spat, which have an organic periostracum over each valve; ostracods, which have a chitinous outer lamella on each valve; and eggs, which are purely organic, have high selective indices. Data again suggest that the captacula are able to detect organic matter and utilize the information for prey selection.

Among the calcareous Foraminifera, *Quinqueloculina* spp. and *Islandiella islandica* are unique, since they have very high selective indices (>6.0), while all other calcareous Foraminifera have selective indices of <3.0. Their selective indices suggest that an additional selection mechanism may be operating.

In the sediment, the captacula must forage through unconsolidated rubble with rough, angular features. If the captacula were able to discern smooth features from rough ones, food selection would be more efficient, since smoothness is often a biological characteristic. The members of the foraminiferal suborder Miliolina (*Quinqueloculina* spp.) have a porcelaneous, imperforate test, while other calcareous Foraminifera (suborder Rotaliina) have perforate tests. The perforations might be detected by the captacula, making the foraminifer less distinguishable from the surrounding sediments. *Islandiella islandica* is the smoothest of the perforate Foraminifera sampled, since its wall perforations are small and the test is globular. *Quinqueloculina* spp. and *I. islandica* may be recognized as food due to their exterior textures and amount of extended cytoplasm; therefore, they comprise a disproportionately large percentage of the prey of *Dentalium entale stimpsoni*.

Small worms and nematodes were seldom ingested, although they were abundant (Table 6). Mobility may account for their escape from the captacula, which they often equal or exceed in size.

The maximum diameter of all food organisms in the sediment and the buccal pouch of *Dentalium entale stimpsoni* in sample 3 was measured. The data were averaged and compared to determine if *D. e. stimpsoni* selects food by size. With the possible exception that *D. e. stimpsoni* may not feed readily on organisms less than 100 μm in diameter, no correlations of food size with food selection were found.

Copepod eggs and empty egg cases were the only food items which averaged less than 100 μm in diameter. The unidentified invertebrate eggs averaged 200 to 250 μm, while all species of Foraminifera averaged at least 150 μm in diameter. Since the possibility of unequal vertical distribution had been previously eliminated, the small size of the copepod eggs and empty egg cases might have been responsible for their negative selection by *Dentalium entale stimpsoni*.

Although diatom tests (composed of amorphous silica) averaged 296/cc of sediment (compared to 94 live Foraminifera/cc), they were absent from the buccal pouches. Determination of probable reasons for negative selection by *Dentalium entale stimpsoni* was not possible.

Specimens of *Dentalium entale stimpsoni* were kept up to 12 weeks in aerated aquaria with sediment from their natural habitat. However, feeding activity probably decreased under laboratory conditions, since the buccal pouches were often empty, or nearly so. Numerous experiments to determine possible feeding mechanisms by *D. e. stimpsoni* were attempted, but none was successful.

The objective of the feeding experiments was to control the food of *Dentalium entale stimpsoni,* and compare predation upon various organisms. A small amount of sediment (2 cc) was used for the experiments, since the mechanics of picking Foraminfera to seed large amounts of sediment would have been prohibitive. The specimens were starved to empty the gut of food, and then placed in the experimental media. There was no evidence of feeding in any of the experiments up to 72 hours. Reasons for the lack of feeding could not be determined, and the experiments were discontinued.

Predatory Pressure: Since Foraminifera are the principal prey of *Dentalium entale stimpsoni,* an estimate of predation by *D. e. stimpsoni* on the foraminiferal populations was attempted. Estimates of the *D. e. stimpsoni* population density, the average number of Foraminifera in the buccal pouches of *D. e. stimpsoni,* and the feeding rate of *D. e. stimpsoni* were necessary for calculation of the predatory pressure at station 3-M.

The population density of *Dentalium entale stimpsoni* was estimated from the results of 30 ponar grabs. Of these, 8 yielded a total of 9 specimens; no evidence of gregarious behavior was found. Since each grab samples 1/20 m^2, the population density of *D. e. stimpsoni* was estimated to be 6/m^2.

Estimates of the foraminiferal population density and the number of Foraminifera per buccal pouch were obtained from sample 3 and 4 data. In the middle slope area, there were an estimated 100 Foraminifera/cc in the upper 2 cm of sediment (Table 1). The population density is therefore 2 000 000/m^2 in the upper 2 cm. The average number of Foraminifera in the buccal pouch of a *Dentalium entale stimpsoni* in sample 3 was 27.

To obtain an estimate of the feeding rate of *Dentalium entale stimpsoni, in situ* experiments would have been the most accurate. However, they were not possible with available time and equipment. Consequently, an estimate could only be obtained by laboratory experimentation.

If the average time necessary for the buccal pouch contents of *Dentalium entale stimpsoni* to pass into the pharynx were known, the number of food organisms consumed per unit time could be estimated. To obtain this estimate, 48 *D. e. stimpsoni* were collected on 9 March 1973 for the following experiment.

The *Dentalium entale stimpsoni* were returned to the laboratory in aquaria with sediment and sea water. In the laboratory they were placed in a sieve (nylon mesh) with 1 mm openings, and suspended in an aquarium of aerated sea water at 10° C, the assumed maximum annual temperature. No sediment was present. At 6 hour intervals, from 6 to 48 hours, groups of *D. e. stimpsoni* were removed and placed in neutralized formalin. The buccal pouch contents of each *D. e. stimpsoni* were later removed, sorted, and counted. The minimum time necessary for half the specimens in a group to have empty buccal pouches was estimated to be the amount of time necessary for the passage of food from the buccal pouch into the pharynx in the average *D. e. stimpsoni.*

The rate of food passage into the pharynx was assumed not to have been affected by the change of depth, orientation, or lack of sediment. It was also assumed that food passed into the pharynx during the experiment at the same rate that it would have if *Dentalium entale stimpsoni* had been able to ingest more food from the sediment.

Three *Dentalium entale stimpsoni* in each of the 30, 36, and 42 hour samples, and 4 in the 48 hour sample had empty buccal pouches. Thus, 30 hours was considered to be the amount of time necessary.

The average 27 Foraminifera found in the buccal pouch of a *Dentalium entale stimpsoni* were estimated to pass into the pharynx in 30 hours. Therefore, in one year, 7 884 Foraminifera would be consumed by each *D. e. stimpsoni,* or 47 304 by 6. Since the standing crop of the total foraminiferal population was estimated to be 2 000 000/m^2, and 47 304 would be consumed in one year, only 2.4% of the standing crop would be consumed annually, without considering the reproductive rate of the Foraminifera.

Although the predatory pressure on the total foraminiferal population is low, the possibility remains that the important prey species are heavily preyed upon, due to selective feeding. In sample 3, *Islandiella islandica, Elphidium* spp., and *Cibicides lobatulus* were 37.7%, 17.9%, and 16.4% of the foraminiferal food of *Dentalium entale stimpsoni,* respectively. Since an estimated 47 304 Foraminifera are consumed by 6 *D. e. stimpsoni* annually, approximately 17 834 *I. islandica,* 8 467 *Elphidium* spp., and 7 758 *C. lobatulus* are consumed per square meter. There are an estimated 16 000 *I. islandica,* 222 000 *Elphidium* spp., and 186 000 *C. lobatulus* per square meter in the upper 2 cm of sediment (sample 3 data). Hence, the percentage of each species' standing crop foraged annually is 11.1, 3.8, and 4.2, respectively. While predatory pressure on *Elphidium* spp., *C. lobatulus,* and the total foraminiferal population is low, *D. e. stimpsoni* exerts a relatively high pressure on its important prey, *I. islandica.* Since *I. islandica* constitutes more than $\frac{1}{3}$ of the foraminiferal food, its population density could be a factor limiting the increase of the population density of *D. e. stimpsoni* at the middle slope area of the Damariscove Island station.

None of the other prey species is preyed upon heavily enough, or constitutes a high enough percentage of the food of *D. e. stimpsoni* to be a limiting factor. The reproductive rates of *I. islandica* and other Foraminifera are not known (PHLEGER, 1960), and this precludes further speculation.

CONCLUSIONS

In the Boothbay region of the Gulf of Maine, *Dentalium entale stimpsoni* Henderson is found in sandy sediments, where the species diversity and density of the macrobenthos are moderate. The foraminiferal prey of *D. e. stimpsoni* is more diverse in the sandy sediments than in the adjacent coarser (gravel) or finer (silt and clay) sediments, while having a fairly high population density. The calcareous Foraminifera, adapted to coarse sediments, and the agglutinated Foraminifera, adapted to fine sediments, are both present in the sandy sediments, causing a moderately high population density concurrent with a high relative species diversity.

Most of the prey of *Dentalium entale stimpsoni* are calcareous Foraminifera; very few are agglutinated Foraminifera. *Cribrostomoides* spp., the only agglutinated foraminifer actively selected as food, is not present in sufficient numbers in any of the sediments to be an important food source.

The absence of *Dentalium entale stimpsoni* in fine sediments reflects the absence of suitable food. Although suitable food is present in coarse sediments, the high percentage of gravel may make burrowing difficult and be responsible for the absence of *D. e. stimpsoni*; the species is restricted to sandy sediments where burrowing is possible and suitable food is abundant.

Sensory cells on the surface of the captacula could be responsible for prey selection, enabling *Dentalium entale stimpsoni* to be a selective feeder. The presence of organic matter (cytoplasm, chitin, etc.) probably initiates prey selection, and its absence probably results in rejection. Organisms which are completely organic (eggs) are readily eaten, as are partially organic organisms (living Foraminifera, bivalve spat, ostracods, etc.). Inorganic particles (sand, empty foraminiferal tests, empty bivalve and ostracod valves, etc.) are consistently rejected. Species of agglutinated Foraminifera which have little organic cement are seldom ingested, while those with a high percentage of organic cement are frequent prey.

The predatory pressure by *Dentalium entale stimpsoni* on the total foraminiferal population is estimated to be 2.4% of the standing crop annually. Due to the selective feeding habits of *D. e. stimpsoni*, an estimated 11.1% of the standing crop of *Islandiella islandica*, the most important food organism, is consumed annually. Since *I. islandica* constitutes 37.7% of the foraminiferal prey of *D. e. stimpsoni*, it is possible that the population density of *D. e. stimpsoni* (6/m²) cannot increase significantly because the most important prey organism cannot maintain its population density under heavier predation.

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